

A REVIEW OF THE INDO-AUSTRALIAN SUBGENUS *PARAZEUGODACUS* SHIRAKI OF *BACTROCERA* MACQUART (DIPTERA: TEPHRITIDAE: DACINAE)

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Abstract

The *Bactrocera* Macquart subgenus *Parazeugodacus* Shiraki, 1933 (= *Melanodacus* Perkins, 1937, syn. n.) is reviewed and eight species included: *B. (P.) abbreviata* (Hardy), *B. (P.) bipustulata* Bezzi, *B. (P.) matsumurai* (Shiraki) and *B. (P.) pendleburyi* (Perkins) from Asia, *B. (P.) terminifer* (Walker) from Sulawesi, *B. (P.) satanellus* (Hering) from Papua New Guinea, *B. (P.) nigra* (Tryon) from Australia and *B. (P.) fulvifacies* (Perkins) from New Caledonia. Four of these species are newly transferred: *B. fulvifacies* from subgenus *Zeugodacus* Hendel, *B. nigra* and *B. satanellus* from subgenus *Melanodacus* and *B. terminifer* from subgenus *Paradacus* Perkins. Primary larval hosts are the fruit of olives (Oleaceae). Three Asian species currently included in *Parazeugodacus*, viz. *B. arisanica* (Shiraki), *B. fulvosterna* Drew & Romig and *B. tetrachaeta* (Bezzi), are transferred to subgenus *Hemizeugodacus* Hardy. Morphological characters suggesting monophyly of genus *Bactrocera* are discussed, with those (plus host plant data) used to support a suggested elevation of *Zeugodacus* to genus all homoplasious.

Introduction

Recognition of subgenera has long been a feature of the economically important and closely related fruit fly genera *Dacus* Fabricius and *Bactrocera* Macquart. Within *Bactrocera* two distinct lineages are present (Drew 1989) – (1) the *Bactrocera* and *Queenslandacus* groups of subgenera, characterised by a deep posterior emargination to the male fifth sternite (apomorphy), and (2) the *Melanodacus* and *Zeugodacus* groups of subgenera, characterised by a (plesiomorphic) shallow emargination.

Within these lineages, subgenera traditionally have been defined by the presence or absence of certain setae and male characters such as the length of the posterior lobe of the surstylus and presence or absence of a pecten (row of cilia) on the third abdominal tergite. Most of these, particularly the setal and pecten characters, are now known to be homoplasious and of little value in determining placement of atypical species (Hancock and Drew 2006).

The publication of a comprehensive revision of Southeast Asian species by Drew and Romig (2013), together with that of Australian-Oceanian species by Drew (1989), means it is now possible to reassess subgeneric limits and define them as (probable) monophyletic units, thereby enabling a better understanding of their relationships and biogeography. This paper deals with subgenus *Parazeugodacus* Shiraki (including *Melanodacus* Perkins, here considered inseparable), which is redefined to contain eight described species distributed from India to New Caledonia. To avoid unnecessary confusion here and with both previous and future studies, *Melanodacus* is retained as the group name until the relationships of *Tetradacus* Miyake are better understood.

Genus *Bactrocera* Macquart
Subgenus *Parazeugodacus* Shiraki

Parazeugodacus Shiraki, 1933: 107. Type species *Parazeugodacus matsumurai* Shiraki, 1933, by original designation.

Melanodacus Perkins, 1937: 57. Type species *Dacus niger* Tryon, 1927, by original designation. **Syn. n.**

Definition. Abdominal sternite V of male with a shallow posterior emargination; posterior lobe of male surstylus short; pecten of cilia present or absent on abdominal tergite III of male; postpronotal setae absent; supra-alar setae present; prescutellar acrostichal setae present; two pairs of scutellar setae; wing pattern reduced, the costal band usually very narrow or absent beyond apex of vein R_{2+3} and usually weak or absent in cell r_1 ; anal streak absent or narrow and largely confined to cell bcu ; occiput black; scutum black with lateral presutural and medial postsutural yellow vittae absent and lateral postsutural yellow vittae short and triangular or absent; when present the vittae do not extend across the transverse suture anteriorly.

Response to male lures. Cue-lure (2 species) or none known (6 species).

Included species. *B. abbreviata* (Hardy), *B. bipustulata* Bezzi, *B. fulvifacies* (Perkins), *B. matsumurai* (Shiraki), *B. nigra* (Tryon), *B. pendleburyi* (Perkins), *B. satanellus* (Hering) and *B. terminifer* (Walker).

Host plants. Wild olives (Oleaceae), with a few records from *Symplocos* (Symplocaceae) and other families. Four of the eight species have been reared from wild olives and cultivated olives are a potential host.

Comments. As is normal with *Bactrocera* subgenera, the defining characters of *Parazeugodacus* are individually homoplasious and it is their unique combination that defines it. Subgenus *Melanodacus* differed solely in the absence of the pecten of cilia and the two are therefore regarded as synonyms, supported by their host plant use. The relationship between *Parazeugodacus* and the other largely Oleaceae-feeding subgenus, the primarily Afrotropical *Daculus* Speiser, requires further investigation. The inclusion of *Parazeugodacus* in the *Melanodacus* group follows the first clear definition of the subgenus by Drew and Romig (2013).

Included species

For detailed morphological descriptions of all species and illustrations of all except *B. terminifer* see Drew (1989) and Drew and Romig (2013). The wing of *B. terminifer* was figured by Hardy (1959).

B. (Parazeugodacus) abbreviata (Hardy, 1974)

Dacus (Zeugodacus) abbreviatus Hardy, 1974: 44. Type locality Laguna, Luzon, Philippines.

Bactrocera (Parazeugodacus) abbreviata (Hardy): Drew and Romig 2013: 243.

Distribution: Southern China (Hong Kong, Yunnan), northern Thailand and Philippines (Luzon).

Host plants: *Chionanthus ramiflorus* and *Olea salicifolia* (Oleaceae) (Allwood *et al.* 1999).

Male lure: None known.

B. (Parazeugodacus) bipustulata Bezzi, 1914

Bactrocera bipustulata Bezzi, 1914: 153. Type locality Mysore, India.

Bactrocera (Parazeugodacus) bipustulata Bezzi: Drew and Romig 2013: 243.

Distribution: Southern India and Sri Lanka.

Host plant: None known.

Male lure: Cue-lure (Drew and Romig 2013).

B. (Parazeugodacus) fulvifacies (Perkins, 1939)

Zeugodacus fulvifacies Perkins, 1939: 32. Type locality Dumbea, New Caledonia.

Bactrocera (Zeugodacus) fulvifacies (Perkins): Drew 1989: 216.

Distribution: New Caledonia (including Lifou and Maré Islands).

Host plant: *Olea paniculata* (Oleaceae) (Amice and Sales 1997, Leblanc *et al.* 2012).

Male lure: Cue-lure (Amice and Sales 1997).

Comments: Lack of information on the male characters of this species (Drew 1972) has resulted in its previous retention in subgenus *Zeugodacus*, where it was placed originally by Perkins (1939). However, examination of photographs of recent material (in Bishop Museum, Honolulu: L. Leblanc pers. comm.) revealed short, blunt surstylus lobes and a shallow sternite V emargination. These and other characters typical of *Parazeugodacus*, including the lack of a postsutural yellow vitta and its host plant, necessitate its transfer to the latter subgenus.

B. (Parazeugodacus) matsumurai (Shiraki, 1933)

Parazeugodacus matsumurai Shiraki, 1933: 107. Type locality Ogasawari I., Bonin Is, Japan.

Dacus boninensis Hardy & Adachi, 1956: 12. Type locality Bonin Is, Japan.

Bactrocera (Parazeugodacus) matsumurai (Shiraki): Drew and Romig 2013: 246.

Distribution: Japan (Bonin Islands).

Host plant: *Osmanthus insularis* (Oleaceae) (Ito 1983).

Male lure: None known.

Comments: A record of *Litsea japonica* (Lauraceae) as the host plant (Drew and Romig 2013) is likely to be a misidentification; the fruits of Oleaceae and

many Lauraceae are very similar and only separable by cross-sectioning the seed. Similarly, the record of *Osmanthus insularis* as a host of the Lauraceae-feeding *B. (Bactrocera) hyalina* (Shiraki) (Drew and Romig 2013) is likely to be a reciprocal misidentification.

B. (Parazeugodacus) nigra (Tryon, 1927)

Dacus niger Tryon, 1927: 211. Type locality Gympie or Cleveland, Queensland, Australia.

Bactrocera (Melanodacus) nigra (Tryon): Drew 1989: 182.

Distribution: Eastern Queensland, from Mossman to the south-east highlands.

Host plants: *Chionanthus ramiflorus* and *Olea paniculata* (Oleaceae) (Hancock *et al.* 2000) and a single record from *Symplocos thwaitesii* (Symplocaceae) (Tryon 1927).

Male lure: None known.

Comments: As with *B. matsumurai*, records of Lauraceae as host plants are misidentifications of Oleaceae, whereas that from *Gomphandra australiana* (Icacinaeae) (May 1953) requires confirmation (Hancock *et al.* 2000). This species lacks the pecten of cilia on abdominal tergite III in males, a character shared with *B. (P.) satanellus*. The synonymy of *Melanodacus* with *Parazeugodacus* results in the transfer of *B. nigra* from the former subgenus.

B. (Parazeugodacus) pendleburyi (Perkins, 1938)

Zeugodacus pendleburyi Perkins, 1938: 141. Type locality Bukit Kutu, Selangor, West Malaysia.

Bactrocera (Parazeugodacus) pendleburyi (Perkins): Drew and Romig 2013: 247.

Distribution: Thailand and West Malaysia.

Host plants: *Symplocos cochinchinensis*, *S. racemosa* (Symplocaceae) and *Gmelina arborea* (Verbenaceae) (Allwood *et al.* 1999), all based on single records with the last requiring confirmation.

Male lure: None known.

B. (Parazeugodacus) satanellus (Hering, 1941)

Melanodacus satanellus Hering, 1941: 48. Type locality Kapakapa, Papua New Guinea.

Bactrocera (Melanodacus) satanellus (Hering): Drew 1989: 184.

Distribution: Papua New Guinea (Central District).

Host plant: None known.

Male lure: None known.

Comments: The synonymy of *Melanodacus* with *Parazeugodacus* results in the transfer of *B. satanellus* from the former subgenus.

B. (Parazeugodacus) terminifer (Walker, 1860)

Dacus terminifer Walker, 1860: 152. Type locality Makassar, Sulawesi.

Dacus (Zeugodacus) terminifer (Walker): Hardy and Adachi 1954: 195.

Bactrocera (Zeugodacus) terminifera (Walker): Drew 1989: 219.

Bactrocera (Paradacus) terminifera (Walker): Drew and Romig 2013: 224.

Distribution: Sulawesi.

Host plant: None known.

Male lure: None known.

Comments: The type and only known specimen is in poor condition and the abdomen is missing. However, the combination of 4 scutellar setae, supra-alar and prescutellar acrostichal setae present, reduced wing pattern and black scutum with no medial and two very short lateral postsutural yellow vittae is characteristic of *Parazeugodacus* and this species is thus transferred from *Paradacus* Perkins. The combination of short lateral postsutural vittae and a totally black face is also seen in *B. (P.) satanellus* but the presence or absence of a pecten is unknown. Hardy and Adachi (1954) also noted its resemblance to *B. (P.) pendleburyi*, which has a similar scutellar pattern.

Excluded species

Three species with a medial postsutural yellow vitta, currently included in subgenus *Parazeugodacus*, are excluded here. Although resembling species within three different species-groups of *Zeugodacus*, their inclusion in that subgenus would require three separate reductions of the posterior surstylus lobes, an unlikely occurrence. The short surstylus lobes and presence of a medial postsutural yellow vitta, plus the presence of four scutellar setae and both supra-alar and prescutellar acrostichal setae, are consistent with the type-species of subgenus *Hemizeugodacus* Hardy, the Australian *B. (H.) aglaiae* (Hardy, 1951). These three species are therefore transferred to that subgenus, as *B. (H.) arisanica* (Shiraki, 1933) from Taiwan, Ryukyu Islands and Thailand, *B. (H.) fulvosterna* Drew & Romig, 2013 from Sarawak and *B. (H.) tetrachaeta* (Bezzi, 1919) from the Philippines. For full descriptions and illustrations see Drew and Romig (2013).

Two subgroups are recognisable within *Hemizeugodacus*. Group A, which includes *B. (H.) aglaiae* and the three species included here, has a medial postsutural vitta and occurs from eastern Asia to Australia. Host plants, known only for *B. (H.) aglaiae*, are *Aglaiia* spp. (Meliaceae) (Hancock *et al.* 2000). Group B contains four species from Papua New Guinea, Solomon Islands and Australia that lack the medial vitta and often have some setae absent, viz. *B. (H.) abdomininigra* Drew, *B. (H.) aurea* (May), *B. (H.) buinensis* Drew and *B. (H.) ektoalangiiae* Drew & Hancock. Known host plants are subspecies of *Alangium villosum* (Alangiaceae) (Hancock *et al.* 2000). These four species possibly belong in a separate subgenus

Neozeugodacus May, currently placed as a synonym of *Hemizeugodacus*. Subgenus *Hemisurstylus* Drew, with its sole species *B. (H.) melanoscutata* Drew, bred from *Garcinia xanthochymus* (Clusiaceae) in New Britain (Drew 1989), appears to be related to group B. Two of the Asian species are attracted to cue-lure (Drew and Romig 2013), while the Australian *B. (H.) aglaiae* and *B. (H.) aurea* are attracted to zingerone, a compound similar to cue-lure (Royer 2015).

Key to *Parazeugodacus* species

- 1 Scutum black without postsutural lateral yellow vittae; fore femora and at least most of mid and hind femora fulvous; anatergite and katatergite both mostly yellow 2
- Scutum black with a pair of short, triangular, postsutural lateral yellow vittae; fore, mid and hind femora fulvous or extensively black; anatergite and katatergite yellow or black 3
- 2 Face fulvous; anepisternal stripe reaching line of anterior notopleural seta; pecten of cilia present on male tergite III (New Caledonia) *B. (P.) fulvifacies* (Perkins)
- Face with a pair of black spots; anepisternal stripe not reaching line of anterior notopleural seta; pecten of cilia absent on male tergite III (Australia) *B. (P.) nigra* (Tryon)
- 3 Face fulvous with two black spots; all femora fulvous with at most their apices fuscous; anatergite and katatergite both mostly yellow 4
- Face blackish at least on lower half; fore femora and at least apical half of mid femora black; anatergite and katatergite yellow or black 6
- 4 Scutellum with only a black basal band (Thailand and Malaysia) *B. (P.) pendleburyi* (Perkins)
- Scutellum with a broad black band from base to apex 5
- 5 Face with a pair of small, rounded black spots; abdomen mostly fulvous with transverse basal black bands on tergites II to IV; fore and mid tibiae mostly pale fuscous (Bonin Is, Japan) *B. (P.) matsumurai* (Shiraki)
- Face with a pair of medium-sized, oval black spots; abdomen mostly black with a black medial band and fulvous areas on posterior of tergite II and submedially on at least tergites III and IV; fore and mid tibiae mostly dark fuscous (SE Asia) *B. (P.) abbreviata* (Hardy)
- 6 Face fulvous on upper half, dark fuscous to black on lower half; mid femur fulvous on basal half; anatergite and katatergite both black (India and Sri Lanka) *B. (P.) bipustulata* Bezzi
- Face and mid femur wholly black; anatergite mostly yellow 7

- 7 Postpronotal lobes black; scutellum with a broad black band from base to apex; hind femur black; anepisternal stripe ending before postpronotal lobe; katatergite black (Papua New Guinea) ... *B. (P.) satanellus* (Hering)
- Postpronotal lobes mostly yellow; scutellum with only a black basal band; hind femur fulvous on basal half, black on apical half; anepisternal stripe reaching postpronotal lobe; katatergite mostly yellow (Sulawesi) *B. (P.) terminifer* (Walker)

Discussion

Biogeography

We recognise six biogeographic zones within the Indo-Australian Region (Fig. 1), each with a high degree of endemism within *Bactrocera* (Table 1).

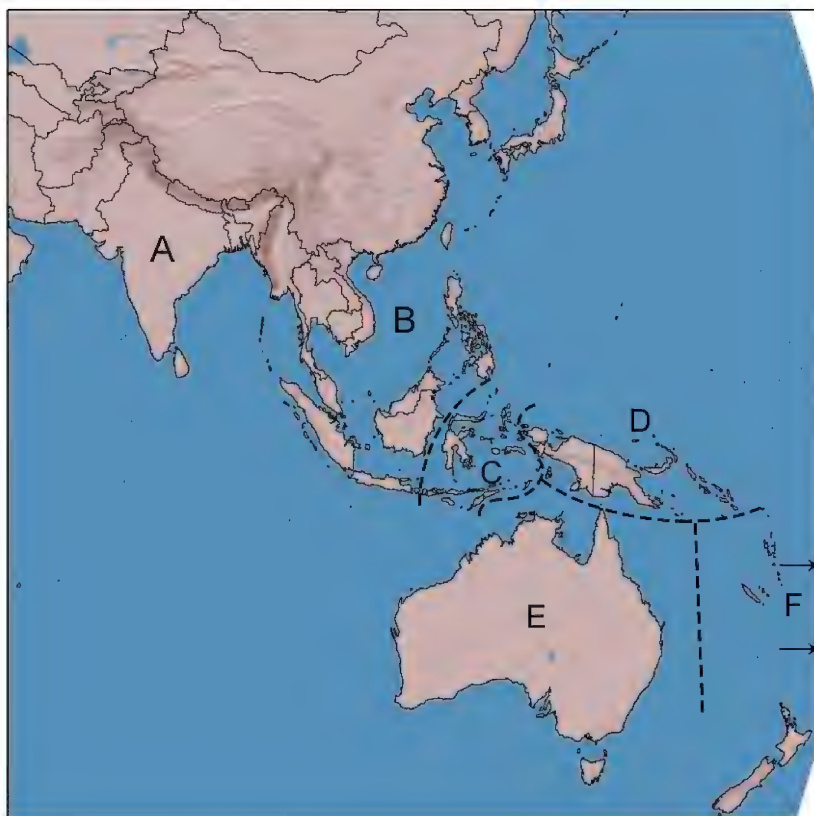


Fig. 1. Biogeographic zones in the Indo-Australian region. A = Indian Subcontinent; B = South-East Asia; C = Wallacea; D = New Guinea; E = Australia; F = South Pacific.

Table 1. Number of species in genus *Bactrocera* and subgenus *Parazeugodacus* in the six recognised biogeographic zones in the Indo-Australian Region, together with the percentage of endemic *Bactrocera* species (all *Parazeugodacus* species are endemic to the particular zone).

Biogeographic Zone	No. species of <i>Bactrocera</i>	% endemic <i>Bactrocera</i>	No. species of <i>Parazeugodacus</i>
(A) Indian subcontinent	74	72	1
(B) South-East Asia	223	84	3
(C) Wallacea	124	82	1
(D) New Guinea	170	85	1
(E) Australia	76	75	1
(F) South Pacific	59	85	1

The eight described species of subgenus *Parazeugodacus* occur largely allopatrically from India and Japan to Australia and New Caledonia and are represented in all six biogeographic zones (Table 1). The four Oriental Region [Zones A-B] species (*bipustulata*, *matsumurai*, *abbreviata* and *pendleburyi*) are individually distinctive and likely represent vicariant speciation. The four Australian Region [Zones C-F] species form two distinct but not necessarily directly related pairs – one with a wholly black scutum (apomorphy) and largely or entirely fulvous face and femora (*nigra* and *fulvifacies*) and one with the short lateral postsutural vittae present, a wholly black face (apomorphy) and largely black femora (*terminifer* and *satanellus*).

Subgeneric relationships

The *Melanodacus* group contains the Afrotropical subgenera *Daculus* Speiser (= *Afrodacus* Bezzi) and *Gymnodacus* Munro, plus the Indo-Australian subgenera *Hemisurstylus* Drew, *Hemizeugodacus* Hardy (= *Neozeugodacus* May) and *Parazeugodacus* Shiraki (= *Melanodacus* Perkins). Molecular evidence (Krosch *et al.* 2012) suggests that typical species of *Paratridacus* Shiraki also belong here (*i.e.* those lacking a medial postsutural vitta and with a relatively short and very broad posterior surstylus lobe, including the type-species).

The *Bactrocera*, *Melanodacus* and *Zeugodacus* groups all appear to be derived from the ancestral subgenus *Tetradacus*. Within the Dacini (Dacina of some authors), two pairs of scutellar setae occur in most of the species in the *Melanodacus* and *Zeugodacus* groups and that character is a possible synapomorphy within the tribe, regained after an initial reduction to one pair in the ancestral taxon (*Ichneumonopsis* Hardy or *Monacrostichus* Bezzi). If two pairs of scutellar setae were to be considered plesiomorphic for the tribe, then independent loss of the basal pair would be required in the ancestral species of each of the five outgroups (*Ichneumonopsis*, *Monacrostichus*,

Dacus, *Tetradacus* and *Bactrocera* group), rather than a single reacquisition in the ancestor of the *Melanodacus*+*Zeugodacus* groups followed by some secondary losses. White (2006) also noted the tendency for ‘lost’ setae to reappear within the Dacini and the exceptional occurrence of four scutellar setae in some specimens of *B. (Bactrocera) quadrisetosa* (Bezzi) is certainly homoplasious. In two unrelated subgenera, *Notodacus* Perkins (*Bactrocera* group) and *Heminotodacus* Drew (*Zeugodacus* group) (and also, weakly, in *B. (Zeugodacus) hatyaiensis* Drew & Romig), postpronotal setae reappear.

Ecological and morphological characters used to support a suggested relationship between *Zeugodacus* and *Dacus* (White 2006, Virgilio *et al.* 2015), viz. shared Cucurbitaceae host plants, presence of a postsutural medial yellow vitta and presence of notopleural vittae or spots along the anterior margin of the transverse suture, are all homoplasious and occur also in the *Bactrocera* group. Cucurbitaceae (and Passifloraceae, another widespread *Dacus* host plant) are major hosts of *B. (Bactrocera) bryoniae* (Tryon) (Hancock *et al.* 2000). A postsutural medial vitta occurs in subgenera *Hemizeugodacus* (*Melanodacus* group), *Apodacus* Perkins (*B. visenda* (Hardy), *B. cheesmanae* (Perkins) and *B. neocheesmanae* Drew), *Bulladacus* Drew & Hancock, *Notodacus* Perkins (all *Bactrocera* group) and *Tetradacus* (Drew 1989, Drew and Romig 2013). A notopleural sutural spot occurs in subgenera *Hemizeugodacus* (two of the three species here removed from *Parazeugodacus*), *Bulladacus* and *Notodacus*, in *B. (Bactrocera) digressa* Radhakrishnan and in *B. (Tetradacus) brachycera* (Bezzi), while a notopleural vitta occurs in *B. (Tetradacus) minax* (Enderlein) and the Australian *B. (Bactrocera) mendosa* (May) (Drew 1989, Hancock 2009, Drew and Romig 2013). Occurrence of the morphological characters in both *Dacus* and *Tetradacus* (and also in *Monacrostichus*) suggests that they are plesiomorphies present in the common ancestor of *Dacus* + *Bactrocera*.

Non-cucurbitaceous host plants also occur in several subgenera within the *Zeugodacus* group (Drew 1989, Drew and Romig 2013) and the use of cucurbits, as in *Dacus*, is likely to represent a secondary shift away from tropical fruit (ancestral *Zeugodacus* group) or asclepiad pods (ancestral *Dacus*: see Hancock and Drew 2006). Further evidence for this is provided by several polyphagous species of *Zeugodacus*, especially *B. (Z.) cucurbitae* (Coquillett) and *B. (Z.) tau* (Walker), reared from 8-11 plant families other than Cucurbitaceae (Allwood *et al.* 1999). Many of these non-cucurbitaceous hosts are also utilised by typical *Bactrocera* species but not by *Dacus*, which is recorded only from Apocynaceae (primarily subfamily Asclepiadoideae), Cucurbitaceae and Passifloraceae (Hancock and Drew 2006). Thus, ecological and morphological characters do not support the raising of *Zeugodacus* from subgenus group to genus as proposed by Virgilio *et al.* (2015) [who, based on diagnoses prior to Drew and Romig (2013) and without examining material, included *Parazeugodacus* within it but left *Melanodacus* in *Bactrocera s.s.*], leaving only molecular evidence that is

weakly supported by low Bayesian PP and ML bootstrap support values at all critical nodes on the resulting (and non-congruent) consensus trees.

Monophyly of genus *Bactrocera* is suggested by the presence of a distinct, black, T-shaped marking on the abdomen, generally accompanied by black lateral markings on tergites III-V that are often divided into discrete rectangular or triangular anterolateral patches. These markings, contrasting strongly with the pale areas of the abdomen, occur in many species in the *Bactrocera*, *Melanodacus* and *Zeugodacus* groups of subgenera and also in subgenus *Tetradacus* but are not seen elsewhere in the Dacinae (including the tribes Gastrozonini and Ceratitidini) and appear to be a synapomorphy for the genus. Dark abdominal markings in *Dacus*, where they occur, are diffuse and not clearly demarcated. Black scutellar apical spots or medial bands are also a recurring character in the *Bactrocera*, *Melanodacus* and *Zeugodacus* groups, as is the reappearance of prescutellar acrostichal setae in most of the species in all three groups; these are also possible synapomorphies within *Bactrocera*, being absent in all species of *Ichneumonopsis*, *Monacrostichus*, *Dacus* and subgenus *Tetradacus*. Within the genus only the *Bactrocera* group (including *Queenslandacus* Drew) appears to have the deep emargination to male sternite V and only the *Zeugodacus* group appears to have a long, narrow and often finger-like posterior surstylus lobe (each of which is regarded as a synapomorphy for those groups). However, since both states also occur within *Dacus* (Munro 1984) neither is suitable for characterising genera. The *Melanodacus* group retains plesiomorphic states of both characters (*i.e.* shallow sternite V emargination and short surstylus lobes) and therefore is not necessarily monophyletic. The subgenera we currently recognise and the number of included species are listed in Table 2.

Table 2. List of subgenera in genus *Bactrocera* (*sensu* Drew 1989, Drew and Hancock 1999, Drew and Romig 2013, Hancock 2015), with the number of species we currently include. Note that *Paratridacus* and *Parazeugodacus* are included in the *Melanodacus* group and *Queenslandacus* is included in the *Bactrocera* group, while *B. superba* Drew & Romig is of uncertain affinity and left unplaced.

Subgenera	African species	Asia-Pacific species
<i>Bactrocera</i> Group		
<i>Apodacus</i> Perkins	0	3 ¹
<i>Bactrocera</i> Macquart	2 ²	ca 380
<i>Bulladacus</i> Drew & Hancock	0	21
<i>Calodacus</i> Hancock	0	6
<i>Notodacus</i> Perkins	0	3
<i>Queenslandacus</i> Drew	0	1
<i>Semicallantrya</i> Drew	0	5 ³
<i>Trypetidacus</i> Drew	0	1

Subgenera	African species	Asia-Pacific species
Melanodacus Group		
<i>Daculus</i> Speiser	8	0
<i>Gymnodacus</i> Munro	2	0
<i>Hemisurstylus</i> Drew	0	1
<i>Hemizeugodacus</i> Hardy	0	8 ⁴
<i>Paratridacus</i> Shiraki	0	7 ⁵
<i>Parazeugodacus</i> Shiraki	0	8 ⁴
Tetradacus – ancestral subgenus?		
<i>Tetradacus</i> Miyake	0	7 ⁶
Zeugodacus Group		
<i>Aglaodacus</i> Munro	1 ⁷	0
<i>Asiadacus</i> Perkins	0	7
<i>Austrodacus</i> Perkins	0	4
<i>Diplodacus</i> May	0	1
<i>Hemigymnodacus</i> Hardy	0	2
<i>Heminotodacus</i> Drew	0	1
<i>Hemiparatridacus</i> Drew	0	1
<i>Javadacus</i> Hardy	0	8 ⁸
<i>Nesodacus</i> Perkins	0	1
<i>Niuginidacus</i> Drew	0	1
<i>Papuodacus</i> Drew	0	6
<i>Paradacus</i> Perkins	0	6 ⁹
<i>Parasinodacus</i> Drew & Romig	0	15 ¹⁰
<i>Sinodacus</i> Zia	0	19
<i>Zeugodacus</i> Hendel	1 ¹¹	120

¹Three Australian and New Guinea species with narrow, slit-like ceromata: *B. visenda* (Hardy), *B. cheesmanae* (Perkins) and *B. neocheesmanae* Drew. ²The two African species (*B. zonata* (Saunders) and *B. invadens* Drew, Tsuruta & White) are introductions from India. ³Includes *B. toxopeusi* (Hering) from Papua Province, Indonesia. ⁴This study. ⁵Four additional Papua New Guinea species belong in either *Austrodacus* (*B. alampeta* Drew, *B. atrisetosa* (Perkins) and *B. unichromata* Drew) or *Zeugodacus* (*B. mesonotaita* Drew). ⁶Includes *B. mesonotochra* Drew, *B. neopagdeni* Drew and *B. pagdeni* (Malloch) from Papua New Guinea and Solomon Islands. ⁷The Madagascan *B. (A.) nesiotis* (Munro). ⁸Two additional Australian species belong in subgenus *Bactrocera*: *B. melanothoracica* Drew and *B. unirufa* Drew. ⁹Three additional Papua New Guinea species belong in *Zeugodacus* (*B. aurantiventer* Drew, *B. citroides* Drew and *B. decipiens* (Drew)). ¹⁰Includes *B. abdopallescens* (Drew) from Papua New Guinea and *B. perpusilla* (Drew) from New Caledonia. ¹¹The sole African species (*B. cucurbitae*) is an introduction from India.

With regard to the phylogeny of *Bactrocera* species presented in Virgilio *et al.* (2015), it should be noted that the Indonesian specimen of *B. dorsalis* (Hendel) used in their analysis is clearly a misidentified *B. papayae* Drew & Hancock (which they placed adjacent to it), since only the latter is known to occur in Indonesia. The two ‘*Afrodacus*’ species used in the analysis (taken from Krosch *et al.* 2012), *B. jarvisi* (Tryon) and *B. minuta* (Drew), were both transferred to subgenus *Bactrocera* by Copeland *et al.* (2004). The specimen of *B. unirufa* Drew used in the analysis (also taken from Krosch *et al.* 2012) is likely to be a misidentification of *B. melanothoracica* Drew, a species with a very variable scutal pattern (Royer and Hancock 2012). Placement of both these species in subgenus *Bactrocera* (as inferred by Virgilio *et al.* 2015) is supported by the deep emargination to sternite V and the produced but still relatively short posterior surstylus lobe in males.

Full justification for the subgeneric transfer of species indicated in Table 2 will occur in future papers in this series; most are a result of improved subgeneric diagnoses in Drew and Romig (2013).

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